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Lintunen, Anna

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Belowground hydraulic conductance in a mature boreal Scots pine tree

Anna Lintunen[1,2], Teemu Paljakka[2], Yann Salmon[1] and Teemu Hölttä[2]

[1]Department of Physics, P.O. Box 68, FI-00014 University of Helsinki, Helsinki, Finland.
[2]Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Helsinki, Finland.

Abstract

We studied the dynamics of belowground hydraulic conductance (k_{bg}) of a mature Scots pine tree in field conditions using continuous xylem diameter change and sap flow measurements over a full growing season in a boreal environment. Our aim was to analyze how k_{bg} is linked to soil temperature and soil water content. k_{bg} was calculated as the ratio of daily maximum sap flow rate to the difference between stem and soil water potential estimated from daily diameter variations of xylem measured with point dendrometers. k_{bg} increased with increasing soil temperature in spring and autumn when soil temperatures were below +8˚C. k_{bg} increased also with increasing soil water content if soil temperature was high enough as was the case in summer. The results suggest that k_{bg} in the studied tree was more limited by soil temperature than water content.

Keywords: cost of water, hydraulic conductance, *Pinus sylvestris*, point dendrometer, sap flow

INTRODUCTION

For plants, water loss and CO_2 assimilation are tightly coupled as both occur through the same stomatal pores in leaves. The loss of water from the leaves to the atmosphere is replaced with sap flow from the soil through the xylem transport tissue. Understanding tree water use and water balance is important as photosynthetic production and tree growth are limited by the capacity of trees to extract water from the soil and transport it to leaves. Belowground hydraulic conductance (k_{bg}) is one of the least understood component of the hydraulic pathway between soil and atmosphere. While k_{bg} has been measured for smaller plants (e.g. Running and Reid, 1980; BassiriRad et al., 1991; Nobel et al., 1990) and tree seedlings of various species in laboratory (e.g. Day et al., 1991; Wan et al. 1999, 2001; Cochard et al., 2000; McLean et al., 2011), it has seldom been measured continuously for mature trees in field conditions (Martínez-Vilalta et al., 2007; McElrone et al., 2007).

Hydraulic conductance is defined as the flow rate per unit pressure driving force, and the driving force in the case of belowground hydraulic conductance is the water potential difference between the stem base and the soil. In the approach introduced by Martínez-Vilalta et al. (2007), k_{bg} was calculated as ratio of area-specific sap flow rate and the difference between soil and stem water potentials estimated from xylem diameter at predawn and during the day, respectively. Xylem and whole stem diameter changes are assumed to correlate linearly with stem water potential changes in steady-state conditions (e.g. Irvine and Grace, 1997; Perämäki et al., 2001; Dietrich et al., 2018).

Root water uptake capacity is known to decrease with decreasing soil water content due to decreased soil hydraulic conductance (e.g. Duursma et al., 2008). In addition to soil water content, soil temperature has been found to play a key role in root water uptake capacity especially at low soil temperatures (e.g. Running and Reid, 1980; Bassirirad et al., 1991; Nobel et al., 1990; Day et al., 1991; Wan et al., 1999, 2001; Cochard et al., 2000). For example, Wan et al. (1999) showed with *Populus tremuloides* seedlings that root water flow was decreased by decreasing soil temperature from 20°C downwards. Decrease in water uptake capacity with decreasing temperature cannot be fully explained by increasing water viscosity, but is also due to changes in some other factors such as changes in root metabolism (Wan et al. 2001). In accordance, Cochard et al. (2000) showed with *Quercus robur* saplings that decreasing soil temperature decreased root conductance considerably, and that this decrease could be explained by changes in water viscosity only in temperatures between 35 and 15°C; in colder temperatures, the decrease was steeper and was suggested to be due to changes in membrane fluidity.

Especially in temperatures below 7°C, root hydraulic resistance has been shown to increase exponentially with temperature (Running and Reid, 1980). Possible causes of decreased root conductance in short term are formation of xylem embolism, formation of gels and tyloses, increase in xylem sap viscosity, changes in ionic strength or changes in extraxylary hydraulic conductivity such as aquaporin functioning or changes in turgor pressure (Hacke, 2014). In addition to sap viscosity, we can expect that soil temperature has a strong effect on aquaporin functioning. Aquaporins are channel-forming membrane proteins present in the plasma membranes and they are highly specific for water, thus enabling rapid transmembrane water flow in plants (Johansson et al., 2000; Javot and Maurel, 2002; McLean et al., 2011; Johnson et al., 2014). Water flow via aquaporins is sensitive to temperature in a way that the water channels significantly contribute to water transport only within an optimum temperature region (Murai-Hatano et al., 2008; Ionenko et al., 2010). Physiological activity in general decreases with decreasing temperature (e.g. Way and Oren, 2010), so refilling of xylem embolism and changes in ionic strength might also be affected by temperature.

We studied the dynamics of k_{bg} of a mature Scots pine (*Pinus sylvestris* L.) tree at SMEAR II station in Finland using continuous stem sap flow and xylem diameter change measurements over a full growing season. Our aim was to analyze how soil temperature and soil water content drive k_{bg} in a mature Scots pine in different seasons.

MATERIAL AND METHODS

Study site

We measured a Scots pine tree in a boreal, evergreen coniferous forest at SMEAR II in Hyytiälä (N 61° 50.8' , E 24° 17.7', 180 m.a.s.l.) in year 2013. The vegetation type is *Vaccinium* (Cajander, 1926) and the forest floor is dominated by dwarf shrubs and mosses. The soil type is glacial till. Mean annual precipitation is 700 mm and mean air temperature +4 °C. The measured tree is 55 years old, 18 m high and breast height diameter is 19 cm.

Field measurements

Sap flux density was measured with constant heat dissipation sensor (Granier, 1985). Probe pairs were inserted 4 cm into the xylem (typical conductive depth of sapwood in mature pine trees in the stand) at breast height (1.3m), with a vertical separation of 11cm, and were covered with reflective aluminum shelter. The sensors were located on the northern side of the stem. Sap flow was recorded in minute frequency. Zero sap flow at night was defined as average of seven consecutive nights as suggested by Lu et al. (2004).

The water potential difference between the stem base and the soil was derived from xylem diameter measurements at breast height; stem water potential was assumed to be proportional to xylem diameter (e.g. Irvine and Grace, 1997; Perämäki et al., 2001; Dietrich et al., 2018) and soil water potential linearly proportional to the highest xylem diameter encountered during the night (Martínez-Vilalta et al., 2007). Xylem diameter was measured continuously with linear displacement transducer point dendrometers (Solartron Inc., Model AX/5-0/5, Bognor Regis, West Sussex, UK; accuracy of 1 μm). In addition, relative air humidity, air temperature, soil temperature and volumetric water content in B1 horizon (9-14 cm depth) were measured continuously.

Rainy days (defined as days for which the mean of the 10% lowest values of relative humidity is above 75%) and days with freezing events (defined as days for which the mean of the 10% lowest values of ambient air temperature is below 0°C) were excluded from the analysis. Rainy days were excluded since water uptake directly through the bark can be expected to interfere with the interpretation of the xylem diameter change measurements. Days with a minimum temperature below zero were excluded because freezing events affect both diameter change and sap flow measurements.

Calculation of belowground hydraulic conductance

Belowground hydraulic conductance was calculated as the ratio of daily maximum (mean of the 10 % highest values) of sapwood-specific flow rate to the difference between daily maximum (mean of the 10% highest values) and daily minimum (mean of the 10% lowest values) of xylem diameter. We used daily values as time lags caused by hydraulic capacitance likely disturbs analysis on short-term dynamics (Martinez-Vilalta et al., 2007). K_{bg} was normalized with the maximum value and only k_{bg} calculated when soil temperature started to increase from zero, which corresponds to the time of soil thawing. Belowground hydraulic conductance in this study actually includes in addition to the belowground parts, the stem base below the breast height. However, it seems that Scots pines at SMEAR II station experience drought induced embolism only marginally and thus the conductance should remain the same in the stem base as it is in the roots (Hölttä et al., 2005; Sevanto et al., 2005).

Statistical analysis

First, it was analyzed how soil temperature, season and their interaction variable affect k_{bg}. The seasons were defined so that spring begins when snow melts and continues until the daily minimum (mean of the 10% lowest values) ambient temperature reaches +8˚C. Then summer follows and continues until the daily minimum ambient temperature drops again below +8˚C, after which it is the autumn until the air temperature drops to 0 ˚C. Second, it was analyzed how soil water content, season and their interaction variable affect k_{bg}. Third, it was analyzed how soil temperature, soil water content, season and their interaction variables affect k_{bg}. The analysis was made with the GLM procedure (SAS Statistical Analysis System) that uses the method of least squares to fit general linear models.

RESULTS AND DISCUSSION

Time series of k_{bg}, soil temperature and soil water content show that after soil temperature increases above zero in the spring, belowground conductance begin to increase and soil water content to decrease towards the summer (Fig. 1). Then in autumn, soil temperature decreases again and soil water content increases, while k_{bg} decreases (Fig. 1).

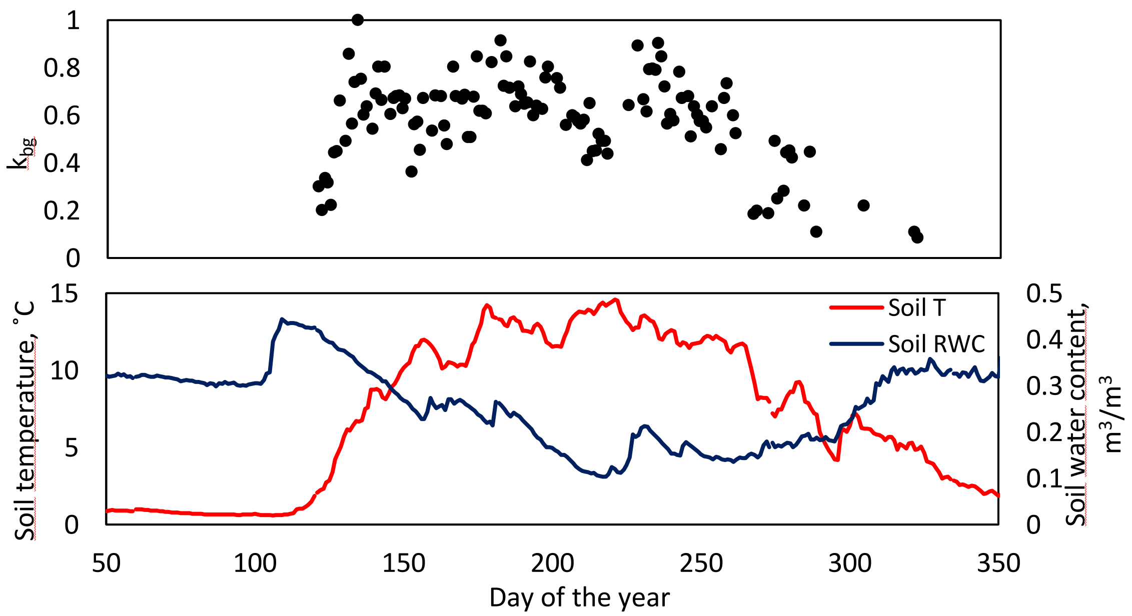

Figure 1. Time series of normalized belowground hydraulic conductance, soil temperature (Soil T) and volumetric soil water content (Soil RWC) in 2013.

Belowground hydraulic conductance was higher in summer than in spring or autumn, but increased with increasing soil temperature more in spring than in summer or autumn (Fig. 2). k_{bg} increased also with increasing soil water content in summer, but the correlation between k_{bg} and soil water content was negative in spring and autumn (Fig. 3). This is because k_{bg} increased with increasing soil water content only if soil temperature was high enough.

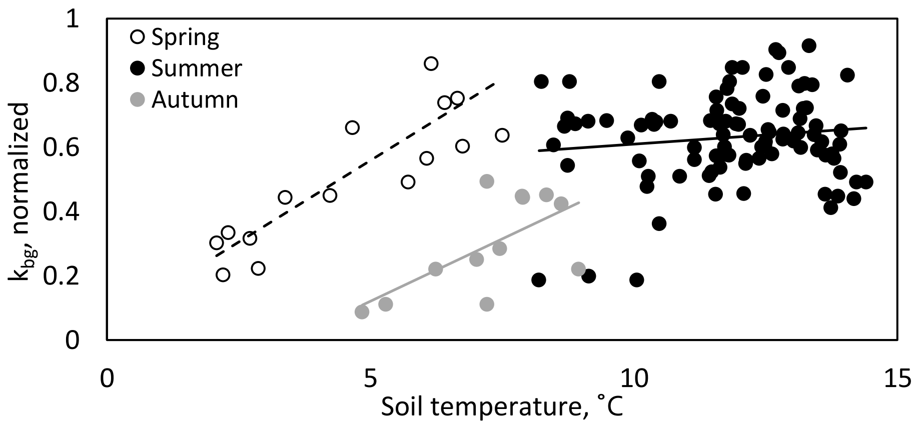

Figure 2. Normalized belowground hydraulic conductance (k_{bg}) plotted against soil temperature in spring (R^2=0.71, y = 0.10x + 0.05), summer (R^2=0.02, y = 0.01x + 0.50) and autumn (R^2=0.42, y = 0.08x - 0.27). Linear fits are drawn for each season.

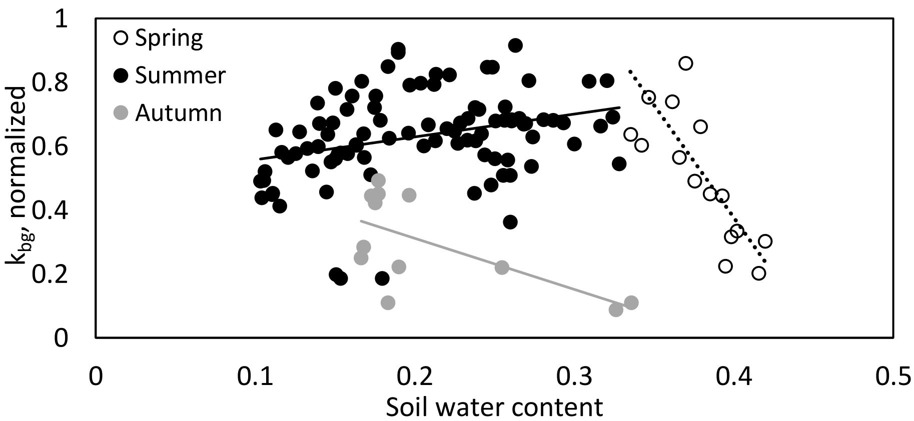

Figure 3. Normalized belowground hydraulic conductance (k_{bg}) plotted against volumetric soil water content in spring (R^2=0.61, y = -7.04x + 3.19), summer (R^2=0.10, y = 0.71x + 0.49) and autumn (R^2=0.42, y = -1.60x + 0.63). Linear fits are drawn for each season.

k_{bg} during spring and autumn was limited by soil temperature, and by soil water content in summer. Especially during spring, the correlation between soil water content and k_{bg} was strongly negative due to cold soil. We also found a steeper decrease of k_{bg} with decreasing soil temperature in spring, when soil temperature is below +8°C. Belowground hydraulic conductance is increasing with increasing temperature likely due to decreasing viscosity and increasing aquaporin activity (e.g. Javot and Maurel, 2002). Also new root tips and mycorrhizas grow in spring when soil temperature increases above a certain threshold temperature, and the number of mychorrizas per root length have been shown to increase with increasing soil temperature in the root system of *Pinus sylvestris* seedlings (Domisch et al. 2002) thus increasing k_{bg}.

As soil temperature affects the uptake and transport of water in the roots, soil water content has a strong effect on the accessibility of water for the roots. Soil matric potential and hydraulic conductivity decreases with decreasing soil water content thus leading to decreased root water uptake (Lobet et al., 2014).

Unlike the present study, Martinez-Vilalta et al. (2007) found no clear relations between k_{bg} and soil temperature or soil water content. However, their data was measured in Scotland from mid-August to November. The climate in Scotland is temperate and oceanic, and their measurements were done in late summer and autumn. The studied coniferous stand was located in boreal environment that can be characterized as cold and moist. Temperature easily dropped below +5˚C in spring and autumn, but soil water content did not drop below 0.3 in spring 2013 and never below 0.1 even in summer 2013. Thus both studies together suggests that the scales of soil temperature and soil water content needs to be large enough to induce effect on k_{bg}. The limiting factors likely vary depending on the environment, and would most likely be very different in warm and dry climate.

CONCLUSIONS

It was shown that in the studied mature Scots pine tree, k_{bg} was dependent on soil temperature and water content. Soil temperature was shown to be the limiting factor for k_{bg} in the studied tree during spring and autumn. During summer, soil water content had a positive effect on belowground hydraulic conductance in the absence of low soil temperatures. As this is a pilot study including no repetition on tree individuals, the results should be considered as preliminary results that give direction for further studies.

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